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Seasonal and vertical distribution of a population of soil arthropods: Cryptostigmata

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With 4 figures

Contents

0. Prefatory note

The seasonal and vertical distribution of some micro-arthropod species in a Scots pine forest soil has been described by Usher (1970a, 1971). Whereas the Collembola usually exhibited only one maximum population density per year, often in the autumn, the species of Mesostigmata tended to show a multi-peak seasonal distribution and relatively little synchronisation between species. Taking the groups as a whole, the Mesostigmata exhibited a greater numerical stability throughout the year than the Collembola. Since the Collembola are detritus or fungus feeders and many of the Mesostigmata are predatory, this finding raises the question of whether predators and nonpredators could be expected to have similar or dissimilar seasonal distributions. The present paper analyses the data for 14 species of Cryptostigmata collected during the same period as the Collembola and Mesostigmata previously described (Usher 1970a, 1971).

1. Site, methods and statistical analysis

The mites were collected from the surface 3 cm of soil under a stand of Scots pine (*Pinus sylvestris* L. ssp. *scotica* (Schott) E. F. Warburg) on Cnoc Eoghainn in the Black Wood of Rannoch, Perthshire, Scotland (National Grid Reference NN 551546). The soil is a humus iron podsol with an organic horizon 24 to 30 cm deep and has been more fully described elsewhere (Usher 1970b).

The climate of the site is cold and wet, with mean annual temperature of about 6 °C, the warmest month on average being July and the coldest February. The precipitation averages about 1200 mm per annum, with a slight seasonal cycle since the autumn and early winter, October to January, have a greater precipitation on average than the spring and summer months, March to August. Average values of precipitation and temperature, as well as values during the sampling programme, are illustrated by Usher (1970a).

Thirty-two square soil cores, of side 4 cm, were taken on each of twelve occasions between October 1965 and October 1966. The cores were divided in the laboratory into sections 1 cm thick, and thus mites were extracted from samples of volume 16 cm³. Preliminary sampling indicated that

the surface 3 cm contained at least 95 per cent of the Cryptostigmata population. The actual numbers of Cryptostigmata have been multiplied by $10^4/16$ so that population densities are expressed as numbers per m².

The statistical treatment is similar to that employed in earlier papers on Mesostigmata and Collembola. Thus, the total number of a species in a core, N, is given by:

$$N = \sum_{i=1}^{k} n_i$$

where there are k layers or sections and there are n_i of the particular species in the ith layer. Also the "mean depth", M, is given by:

$$M = \frac{\sum_{i=1}^{k} d_i \, n_i}{N}$$

where d_i is the depth of the centre of the ith layer. A measure of the spread of the species around this statistic of the vertical distribution is given by the "depth deviation", S, which is given by:

$$S = \sqrt{\frac{1}{N}\left\{\sum_{i=1}^{k} n_i \, d_i^2 - \frac{\left(\sum_{i=1}^{k} n_i \, d_i\right)^2}{N}\right\}}$$

As an example, in the Cryptostigmata studies at Rannoch $k = 3$, $d_1 = 0.5$, $d_2 = 1.5$ and $d_3 = 2.5$. On 31 October 1965 there were $n_1 = 49$ *Adoristes poppei* in samples from the surface layer, $n_2 = 11$ in samples from the second layer and $n_3 = 6$ in samples from the third layer. These data give $N = 66$, $M = 0.848$ and $S = 0.639$.

2. Results and discussion

2.0. Prefatory note

Only the 14 most frequently occurring species were counted (table 1). *T. velatus* was particularly abundant since it accounted for about 40 per cent of all Cryptostigmata in the samples. The data of adult and juvenile stages of two species, *C. bipilis* and *P. peltifer*, have been analysed separately so that in figs. 1 and 2 the proportion of juveniles in the populations of these species is shown. For 12 of the species the mean population density and the mean depth are shown in Figs. 1—4, the vertical bars representing one standard error on either side of the mean population density. Two species, *C. segnis* and *C. dentatus*, were insufficiently frequent for statistical analyses of their populations, and hence figs. 1 and 3 show only the mean population density without standard errors or a mean depth.

2.1. Nanhermannia nana

The data for this species are shown in fig. 1b where it will be seen that it occurs relatively deep in the soil profile since the average mean depth over the year was 1.57 cm. ANDERSON (1971) showed that the similar species, *N. elegantula*, occurred in its greatest numbers throughout the fermentation horizon of both Castanea and Fagus woodland soils, whilst WALLWORK (1967) records *Nanhermannia* species as being typical of the more stable environment between the lower litter and humus horizons. VAN DER HAMMEN (1952) considers *N. nana* to have a preference for damp sites. Fig. 1b shows that this species moved deeper into the soil during the winter and during the period of the summer when the surface of the soil became desiccated.

In Britain the species is distributed relatively widely, though it appears to occur most frequently in acidic soil types. WOOD (1967a, 1967b) records it from Malham in Northern England, where it is a characteristic species of his group D. This group of soil arthropods occur in the soils of Festuca-Agrostis and Nardus grasslands, both soils in which fermentation and humus horizons are present. BLOCK (1965) records it from several grassland types at Moor House in Northern England, though its greatest population density is in soils under Nardus grassland. BLOCK (1966a) also illustrates its seasonal abundance in mineral and peat soils, which indicates one clear maximum population density each year in the late summer

Table 1. The species of Cryptostigmata collected during the sampling programme, October 1965 to October 1966

Nanhermanniidae	
Nanhermannia nana (NICOLET)	800
Camisiidae	
Camisia spinifer (C. L. KOCH)	698
C. segnis (HERMANN)	38
Platynothrus peltifer (C. L. KOCH)	3,285
Belbidae	
Porobelba spinosa (SELLNICK)	670
Eremaeidae	
Oribella lanceolata (MICHAEL)	708
Ceratoppia bipilis (HERMANN)	1,406
Carabodidae	
Tectocepheus velatus (MICHAEL)	12,165
Cepheus dentatus (MICHAEL)	95
Liacaridae	
Adoristes poppei (OUDEMANS)	1,358
Notaspididae	
Chamobates schützi (OUDEMANS)	888
Pelopidae	
Eupelops spp.	707
Phthiracaridae	
Steganacarus magnus (NICOLET)	2,784
Phthiracarus piger (SCOPOLI)	589
Total	**26,191**

Note: The nomenclature is based on Willmann (1931), with later generic revisions.
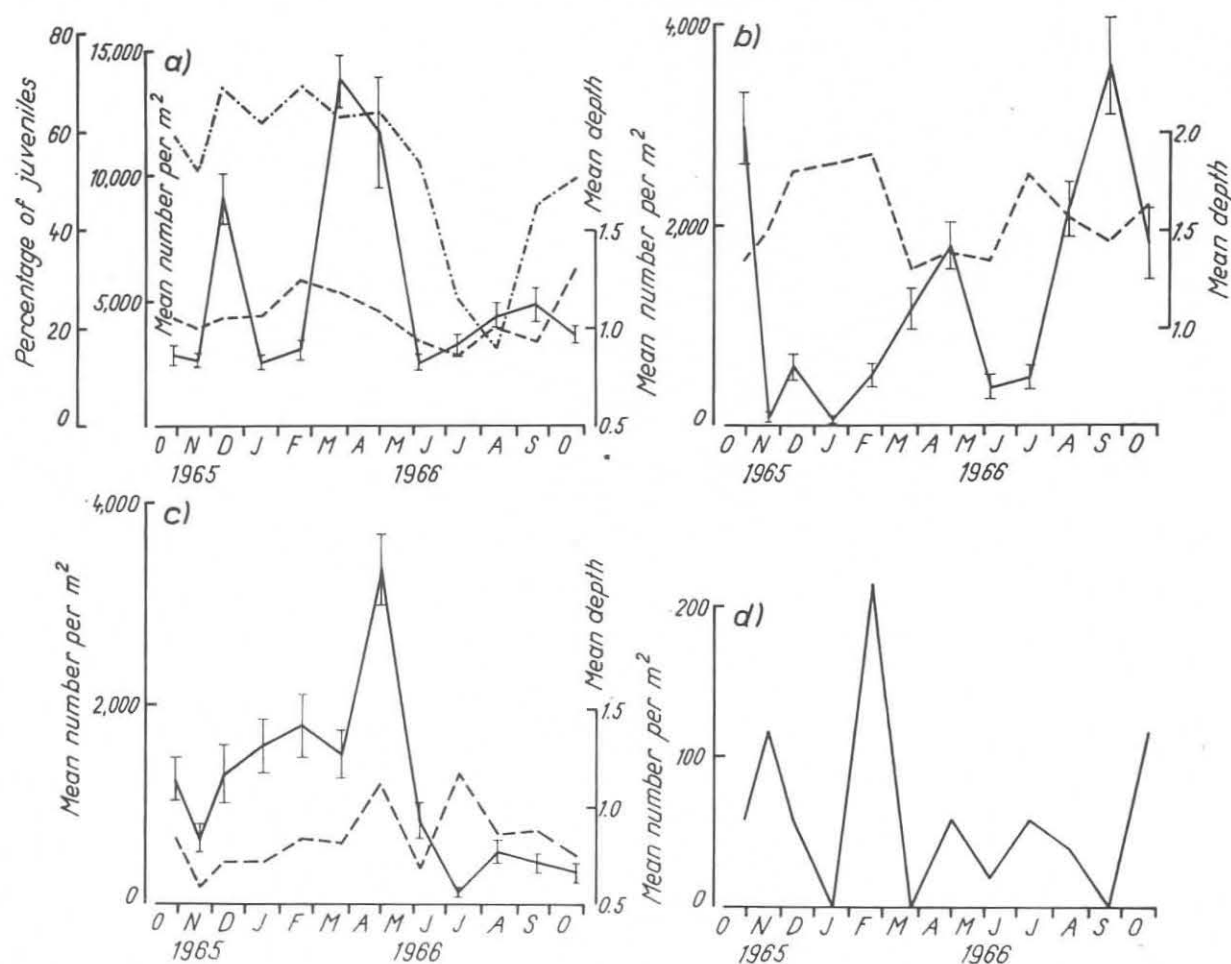

Fig. 1

(varying between July and October) and the possibility also of a smaller maximum in the late winter in February or March. His findings on seasonal distribution are substantially the same as those in fig. 1b where the population maximum occurs during July to October with a smaller maximum in April. A maximum population density in late summer for other *Nanhermannia* species has been demonstrated by MORITZ (1963).

2.2. Camisiidae

There is a considerable difference between the literature on the three species of mites in this family since *P. peltifer* probably has the most extensive literature of all British Cryptostigmata. Studies on the Cryptostigmata have not frequently recorded the two species of *Camisia*, and those that have recorded these species tend to record rather small numbers. LUXTON (1966) did, however, record *C. segnis* as being the dominant mite species in dense *Ammophila* stands on sand dunes. BLOCK (1965a) found *C. segnis* only in the more acid soils of his study area, whilst VAN DER HAMMEN (1952) mentions that the species is arboricolous. WOOD (1967a) found *C. spinifer* only on his more acid sites though BLOCK (1965a) found it on sites with a wide range of pH values. Both species would thus tend to have a wide distribution. At Rannoch, *C. spinifer* would appear to have a maximum population density in the spring and very low population densities during the summer months (Fig. 1c). Although *C. segnis* was uncommon at Rannoch, the data (Fig. 1d) might indicate that this species shows two maximum populations, one in the autumn (October to November) and one in the winter (February). Both species occur predominantly in the litter horizon, and hence their mean depths are small throughout the year (the mean for *C. spinifer* is 0.83 cm).

P. peltifer has been recorded over an extensive geographical area in the Northern Hemisphere (WALLWORK 1967) and from New Zealand (McMILLAN 1969), and throughout much of its range it is a very commonly occurring species (as, for example, in the Netherlands where its distribution is discussed by VAN DER HAMMEN 1952). In Britain the species is common, with BLOCK (1965a) recording it from a wide range of sites although he also shows it to be a characteristic species of Eriophorum bogs and peat that is being recolonized by vegetation (BLOCK 1966b). WOOD (1967a, 1967b) shows it to be a species particularly associated with Nardus grassland, and GIFFORD (1967) recores it from pine forest soils. The species would thus tend to be most frequent in acidic and woodland soils in which there is at least some evidence of fermentation and humus horizons.

The mean depth, shown in Fig. 1a, shows that this is a species of the litter horizon and the surface of the fermentation horizon. This is in agreement with HAARLØV's (1960) results on the vertical distribution of *P. peltifer* in the soil under a hawthorn thicket. Fig. 1a shows that there is virtually no seasonal influence on the mean depth.

In fig. 1a there appears to be single population maximum during the spring (March to May) period. The proportion of juveniles in the population increases in the late summer and autumn (September to October) and remains large throughout the winter until the general decline in the population size in May and June. These observations are in close agreement with published accounts of the phenology of the species (BLOCK 1965b, 1966a; HAARLØV 1960; HARDING 1971; HARTENSTEIN 1962 — though the identification of HARTENSTEIN's material is doubted by JALIL 1972; LUXTON 1967 and MORITZ 1963). Egg production and the appearance of the first larvae in the population is probably temperature dependent. Whereas the proportion of juveniles did not start to increase until September in the Rannoch population (see Fig. 1a), BLOCK (1965b) showed that the larvae appeared in the population in August at his site at Moor House. This site is at approximately the same altitude as the site at Rannoch, but it is situated 220 km south of the Rannoch site. HARDING (1971) showed

Fig. 1. The data for the mean population size, expresses as numbers per m² (continuous lines), and mean depth (dashed lines) for four species, (a) *Platynothrus peltifer*, (b) *Nanhermannia nana*, (c) *Camisia spinifer*, and (d) *C. segnis*. The interval about the mean population size represents one standard error. For *P. peltifer* the proportion of juveniles in the population is also plotted (dotted and dashed line).

that larvae started to appear in his population in Nottinghamshire in late July. His site is situated at a lower altitude than the Rannoch and Moor House sites and is approximately 210 km south of Moor House. These results in widely separated habitats and the subsequent appearance of other stages in the development towards adults accord with the growth rates of *P. peltifer* recorded by JALIL (1972).
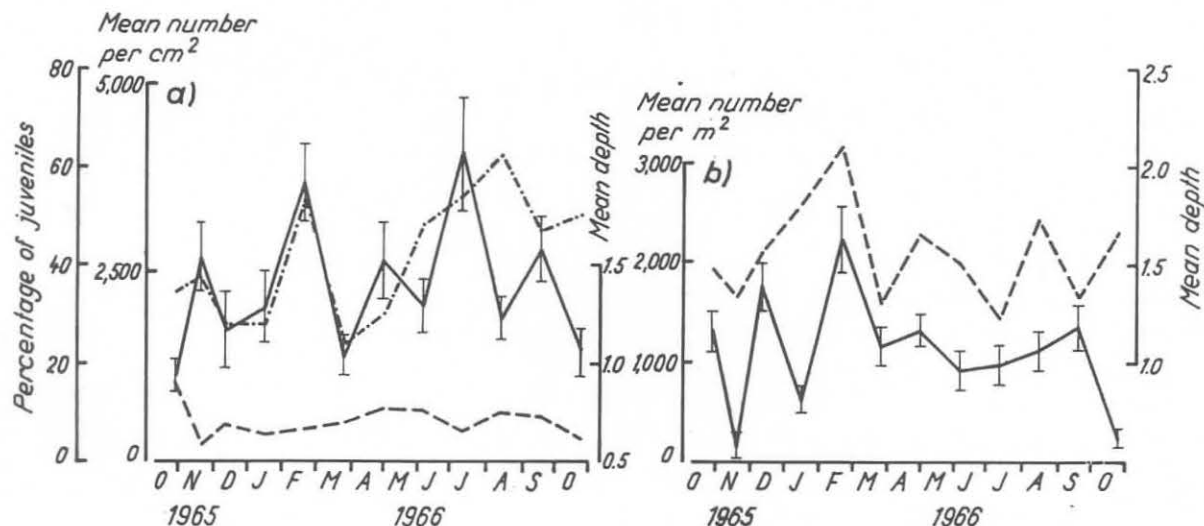

Fig. 2. The data for (a) *Ceratoppia bipilis*, and (b) *Porobelba spinosa*. The lines have the same representation as those in Fig. 1.
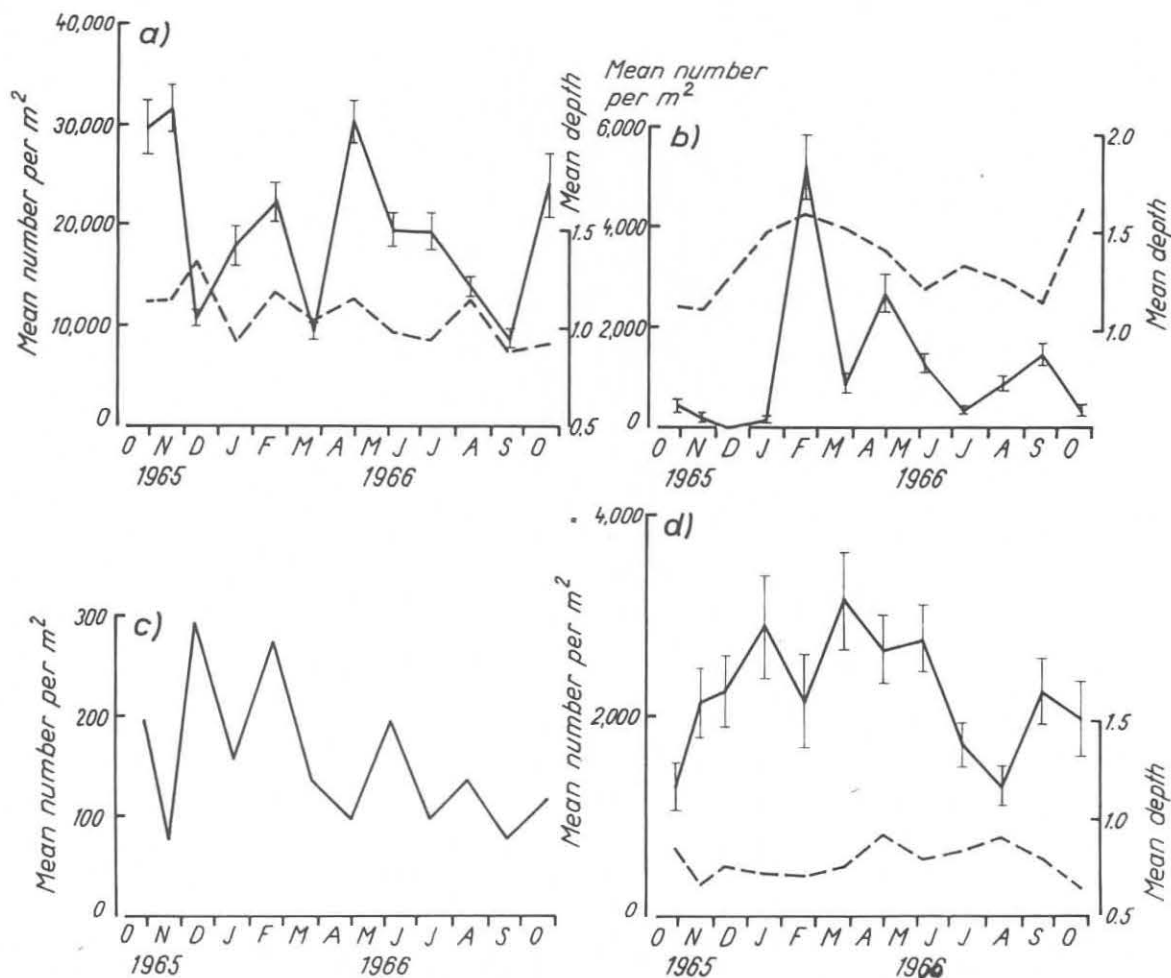

Fig. 3. The data for (a) *Tectocepheus velatus*, (b) *Oribella lanceolata*, (c) *Cepheus dentatus*, and (d) *Adoristes poppei*. The lines have the same representation as those in Fig. 1.

2.3. Porobelba spinosa

The data for *P. spinosa* are shown in fig. 2b where it will be seen that there is no clear seasonal distribution in the abundance of the species although the population size during the winter months is larger than during the summer months. The species has a mean depth of 1.56 cm indicating that it occurs deeper in the soil, below the litter horizon and in the fermentation horizon. There are relatively few records of this species in Britain, though Wood (1967a) recorded it in rather small numbers from several sites of contrasting pH in Northern England.

2.4. Eremaeidae

This family is represented at Rannoch by two species, *C. bipilis* and *O. lanceolata*. Alhough *C. bipilis* has been frequently recorded in Britain it is usually present only in small numbers (Macfadyen 1952).

O. lanceolata has only been infrequently recorded in the British Isles (Curry 1969). Van der Hammen (1952) found *O. lanceolata* in a number of forest and acidic soil types in the Netherlands. The seasonal distribution of *O. lanceolata* at Rannoch, fig. 3b, indicates a single maximum population density in the winter with relatively small populations in summer and autumn. The mites occurred deeper in the soil during the winter and nearer to the soil surface during the summer.

Although *C. bipilis* has an extensive geographical distribution in the Northern Temperate regions (Wallwork 1967), in Britain it tends to be most abundant in acid humus soils. Block (1966b) recorded it in an Eriophorum vaginatum community on peat, Gifford (1967) from Scots pine forest soils and Wood (1967a, 1967b) found it particularly frequent in the Nardus grassland although he also recorded it from Sesleria and Festuca-Agrostis grasslands. At Rannoch *C. bipilis* is a species of the litter layer having an average mean depth throughout the year of 0.71 cm. The mean depth shows no seasonal cycle, and hence it would appear that neither cold nor desiccation induces the species to migrate deeper into the soil. There is no significant difference between the mean depths of adults and juveniles (adult mean depth = 0.72 cm, juvenile mean depth = 0.68 cm). The data on the population, fig. 2a. indicates two maxima during the year, one in the winter and one in the late summer. Juveniles were present in the population throughout the year and their occurrence closely follows the total population size. Minimum numbers of juveniles occurred in December and January and again in April and May and minimum numbers of adults in October. The minimum total population size in April and May is accounted for by a disappearance of juveniles from the samples since the number of adults varied very little.

2.5. Carabodidae

Two species of this family were recorded from Rannoch, *C. dentatus* (fig. 3c), which was relatively uncommon, and *T. velatus* (fig. 3a), which was the most abundant species of micro-arthropod in the soil fauna at Rannoch. *C. dentatus* has not been widely recorded in Britain, but it would appear to be a species of moist (Macfadyen 1952) or acidic (Block 1965) grassland habitats. Indeed, its occurrence in these habitats raises questions about its feeding relationships since Wallwork (1958) lists *C. latus* as a specific feeder and he consider that all Cepheus species are wood feeders (Wallwork 1967). At Rannoch the species was apparently scarce (fig. 3c), though if the adults were feeding within woody remains in the soil the method of extraction would probably have grossly underestimated the actual population. It would appear that there is a single maximum population density, occurring during the winter months.

T. velatus has been widely recorded in Northern Temperate regions (Wallwork 1967) as well as from the Southern Temperate regions (McMillan 1969), and where it occurs it is usually extremely common. In Britain it has been recorded from an extremely wide range of habitats: for example, Luxton (1966) recorded it from sand dunes; Block (1965a, 1966a)

from several different grasslands and from moorland soils (BLOCK 1966b); WOOD (1967a) from many soils types with pH values between 3.5 and approximately neutral, though it was particularly frequent in rendzina and skeletal soils over limestone — it was the only species of Cryptostigmata that is so frequent that it indicated nothing about the soil type (WOOD 1967b); MACFADYEN (1952) records it from several different wet grassland types; DAVIES (1963) from ground being reclaimed after ironstone quarrying; and HARDING (1967) found it frequently associated with cellophane samples inserted in forest soils. There is no doubt that *T. velatus* must be about the most generally distributed species of Cryptostigmata both geographically and in relation to different environments.

The average mean depth for *T. velatus* at Rannoch was 1.06 cm (fig. 3a), indicating that the species occurs in the litter and top of the fermentation horizon. This is in reasonable agreement with the percentages quoted by MURPHY and JALIL (1964) who found 87 per cent of adult *T. velatus* in their L + F horizon. HAARLØV (1960) stated that *T. velatus* had a similar vertical distribution to *P. peltifer*, which at Rannoch also had an average mean depth of 1.06 cm (fig. 1a). These results contrast with WALLWORK'S (1967) statement that *T. velatus* is an example of the "medium- and small-sized species (that) show little or no decided preference for one or other of the organic strata and are frequently found in all layers, except perhaps the upper litter layer". There is some evidence, fig. 3a, that *T. velatus* occurs deeper in the soil in winter than in summer.

The seasonal distribution of *T. velatus* in fig. 3a shows two maximum population densities in October and November and again in May. MURPHY and JALIL (1964) also found two maximum population densities, in November and March, and HAARLØV (1960) recorded a maximum in November and a smaller peak in May. BLOCK's (1966a) graphs for *T. velatus* in mineral soil show October maxima with smaller peaks in February and March, though in peat soils there was a single peak during September to November. Published studies therefore agree that the maximum population density is recorded in October to November with a smaller maximum in late winter or early spring. MURPHY and JALIL (1964) conclude that there are two generations per year, though WALLWORK (1967) indicates that 3—5 generations per year could occur when conditions were favourable.

2.6. Adoristes poppei

There is some doubt as to whether this species is distinct from *A. ovatus* (VAN DER HAMMEN 1952; MARSHALL 1968). *A. poppei* (or *A. ovatus*) has been recorded from Europe and North America, though in Britain it is apparently not common. BLOCK (1965a) records it only from Nardus grassland, and GIFFORD (1967) records it from pine forest soils. Its seasonal distribution, fig. 3d, shows that the maximum population density is reached during the winter months (January to March) with a minimum during the late summer. One maximum population density was also recorded by MORITZ (1963) for *A. ovatus*, though this maximum occurred during the period September to November. It is predominantly a species of the litter layer of the soil, although the mean depth increases during the summer months indicating that its vertical distribution is more a function of desiccation than of temperature.

2.7. Chamobates schützi

This species is very similar to *C. incisus*, with which it has frequently been confused (VAN DER HAMMEN 1952). BLOCK's (1965a, 1966b) studies indicate that it is a species of acidic soil types since it occurred on his Calluna moor as well as on hummock tops and Eriophorum vaginatum communities, although WOOD and LAWTON (1973) collected it for their studies on respiratory rates from the litter layer of a Fagus woodland. At Rannoch, *C. schützi* would appear to reach a maximum population density during the winter, in January of February (fig. 4a). HAARLØV (1960) concluded that *C. incisus* had only one generation per year, and BLOCK's (1966a) data are inconclusive since in one year there was a maximum population density during March to May whereas in the following year this period coincided

with a minimum population density. HAARLØV (1960) also recorded that *C. incisus* was a species characteristic of the surface of the soil profile. At Rannoch the vertical distribution has a pronounced seasonal distribution. Although in spring and autumn *C. schützi* could be considered as occurring predominantly in the litter layer (mean depth about 1.1 cm), during both the cold winter period and the dry summer period the mean depth increased to about 1.5 cm. The vertical distribution would therefore appear to be a function of both temperature and desiccation.
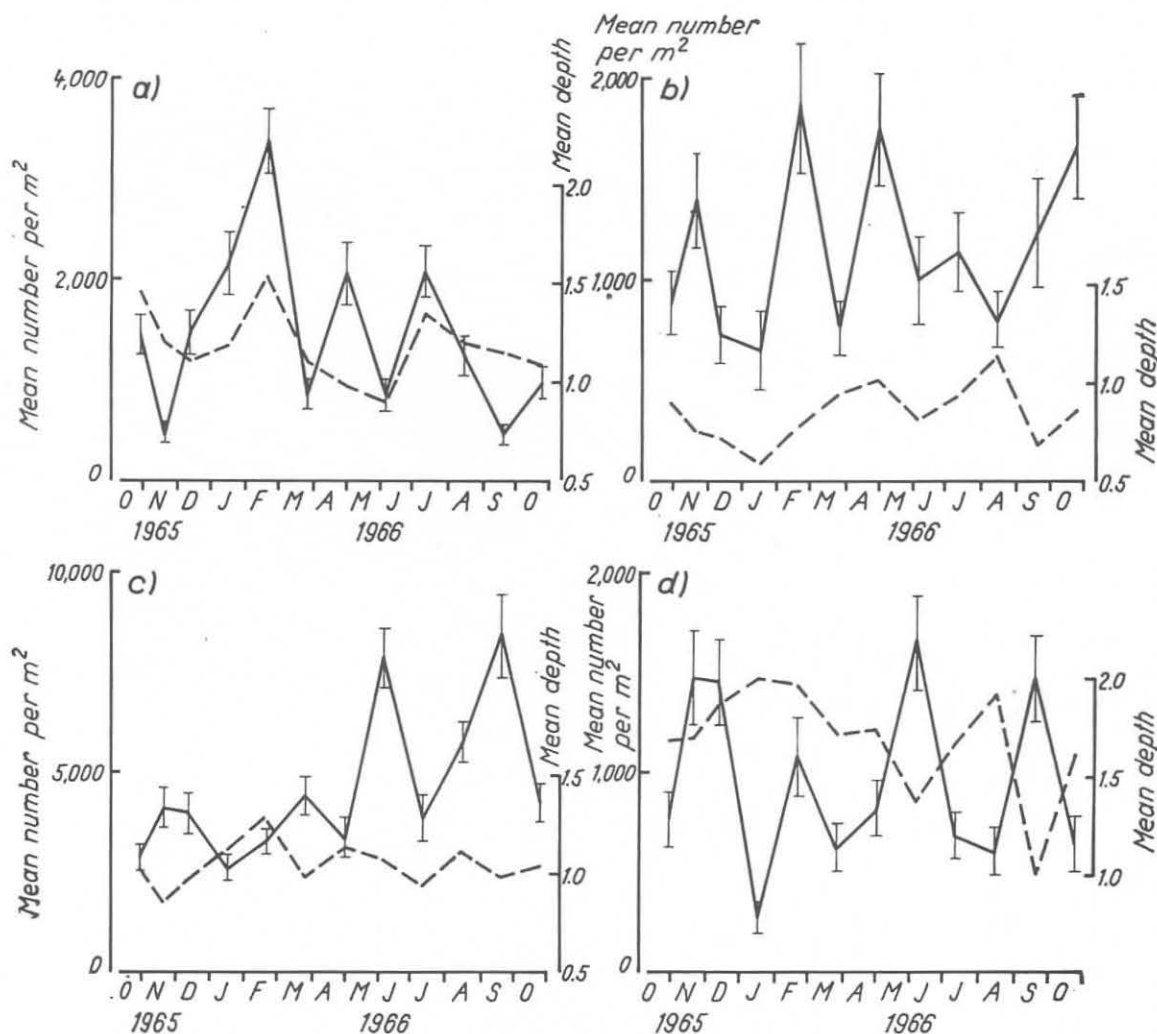

Fig. 4. The data for (a) *Chamobates schützi*, (b) *Eupelops* spp., (c) *Steganacarus magnus*, and (d) *Phthiracarus piger*. The lines have the same representation as those in Fig. 1.

2.8. Eupelops ssp.

The identity of the Rannoch species of *Eupelops* is uncertain, except that at least two species are likely to occur on the site. The numbers collected, fig. 4b, show a considerable oscillation and no seasonal trends. This is possibly due to two or more species being added together. BLOCK (1966a) recorded two species, *E. planicornius* and *E. plicatus*, both of which show a seasonal trend but the two species are not synchronised. It is possible that the *Eupelops* spp. at Rannoch do have a seasonal distribution but that the genus as a whole has no obvious seasonal trend. The species are, however, species of the litter horizon since the average mean depth is 0.84 cm.

2.9. Phthiracaridae

Two species occurred frequently at Rannoch; the seasonal distribution of *S. magnus* is shown in fig. 4c and *P. piger* in fig. 4d. *S. magnus* is the largest species of Cryptostigmata at Rannoch, the adults having a mean liveweight of about 600 µg (WOOD and LAWTON 1973).

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S. magnus tends to occur in acidic soil types. HAYES (1965) and GIFFORD (1967) have recorded it from several coniferous forest soils, and WEBB and ELMES (1971) have recorded it from sandy heathland soils. The species has, however, been recorded from other habitats such as Sesleria grassland (WOOD 1967a) and saltmarsh (LUXTON 1966). At Rannoch, fig. 4c, there is apparently a minimum population density during the winter with maxima in the spring and late summer. Such a seasonal cycle is very similar to that illustrated by CANCELA DA FONSECA (1967), though HAYES (1965) concludes that there are no real seasonal differences. Although WALLWORK (1967) indicates that *S. magnus* may have two generations per year, WEBB and ELMES (1971) show that there are peaks of eggs in June and again in August and that some egg development occurs throughout the year. These two peaks in egg availability, with faster development during the summer and slower development during the winter, might result in the bimodal distribution recorded by CANCELA DA FONSECA (1967) and at Rannoch (fig. 4c).

S. magnus has an average mean depth of 1.04 cm which indicates that the species is characteristic of the litter and surface of the fermentation horizon. This is in agreement with HAYES' (1965) conclusion that *S. magnus* was predominant in the litter, though ANDERSON'S (1971) illustration indicates that the species is most frequent in the surface of the fermentation horizon. At Rannoch the mean depth increased to 1.28 cm in February, the coldest period of the year. ANDERSON's (1971) data indicate that he did not find *S. magnus* in the litter layer during the winter. It would therefore appear that *S. magnus* migrates vertically as a results of temperature, although BERTHET (1964) showed a close correlation between the average daily displacement of mites and the amount of rainfall.

P. piger has been less frequently recorded in Britain though it is known from coniferous woodland soils (HAYES 1965; GIFFORD 1967) and from some moorland and limestone soils (BLOCK 1965a). Very little can be concluded from the seasonal distribution in fig. 4d except that there is a minimum population density during the winter months. WALLWORK (1967) indicated that *P. piger* may have two generations per year. HAYES (1965) states that *P. piger* was "clearly predominant in the litter". At Rannoch, there were few specimens of *P. piger* in the surface 1 cm and the mean depth was usually greater than 1.5 cm. The species is thus characteristic of the fermentation and not the litter horizon at Rannoch. The mean depth varies considerably, and it would appear that *P. piger* is deeper in the soil during the winter months than in the summer and autumn.

3. Summary and conclusions · Zusammenfassung und Schlußfolgerungen

There are three ways of investigating the Cryptostigmata community as a whole. First, it would be possible to examine any synchronization between the numbers of different species, and the numerical stability of the community. Secondly, it would be possible to separate the community according to its vertical stratification in the soil. Thirdly it would be possible to examine the influences acting to alter vertical distribution.

First several patterns of seasonal distribution have been recorded. Apart from *Eupelops* spp. which showed no distribution, nine species showed a single maximum population density in the year and four species showed two population maxima. The Cryptostigmata are thus similar to the Collembola in usually having a single population maximum (USHER 1970a) although they differ in not having the maxima synchronised to the autumnal period. The maxima showed in Figs. 1 to 4 occur during all seasons of the year with the exception of the late autumn and early winter. Similarly, there is no synchronization between the four species with two maxima during the year. The Cryptostigmata community as a whole is therefore numerically stable, the numbers observed varying only twofold, between 1732 in January (925 of these were *T. velatus*) and 3299 in May (when 1548 were *T. velatus*).

Secondly, there was a vertical stratification of the community. Four species, *A. poppei*, *C. bipilis*, *C. segnis*, *C. spinifer* and *Eupelops* spp., were usually found in the litter layer and only occasional specimens were found more than 1 cm deep into the fermentation horizon. All of these species tended to have relatively small depth deviations. Five more species occurred in the litter and surface fermentation horizons, and hence their depth deviations were larger. These species are *C. schützi*, *O. lanceolata*, *P. peltifer*, *S. magnus* and *T. velatus*. A further three species, *N. nana*, *P. piger* and *P. spinosa*, were characteristic of the fermentation horizons.

Thirdly, two factors appeared to be responsible for mites migrating downwards in the soil profile and it seemed unlikely that any factors were causing the mites to migrate upwards. The deeper

layers of the soil, although having a smaller pore space, have a more constant environment, and the two factors determined to cause vertical migration were both extremes of the environment at the litter surface. During the winter the temperature dropped and the litter layer became frozen. Several mites, notably *C. schützi*, *N. nana*, *O. lanceolata*, *P. piger*, *P. spinosa*, *S. magnus* and possibly *T. velatus*, occurred deeper in the soil during this period of the year. During the summer of 1966 there was an unusually small rainfall with the result that the soil became very dry, especially the litter and the surface of fermentation horizons. Some of the mites, *C. schützi*, *N. nana*, *Eupelops*, ssp. and possibly *A. poppei*, occurred deeper in the soil during this dry period. It will be apparent that these two influences, very cold temperature and desiccation of the soil surface, only affect a few species and that they affect not only the species of the litter horizon but also the species such as *N. nana* that are characteristic of the fermentation horizon.

Es gibt (im wesentlichen) drei Möglichkeiten, die Cryptostigmata-Gemeinschaften als Ganze zu untersuchen: (I) Es wäre möglich, die Synchronisation zwischen Artenzahl und numerischer Stabilität der Gemeinschaften zu prüfen. (II) Es wäre möglich, die Gemeinschaften nach der Vertikalverteilung im Boden zu differenzieren. (III) Es wäre möglich, die Einflüsse, die Änderungen der Vertikalverteilung bewirken, zu prüfen.

(I) Verschiedene Arten der jahreszeitlichen Verteilung wurden festgestellt. Mit Ausnahme von *Eupelops* spp., die keinen Massenwechsel erkennen lassen, zeigten neun Arten je 1 Maximum und vier Arten je 2 Maxima im Jahr. Die Cryptostigmata sind in dieser Hinsicht den Collembola ähnlich, die gewöhnlich nur ein einziges Besatzdichte-Maximum haben (USHER 1970a), obwohl sie von diesen verschieden sind, weil sie keine synchronisierten Herbst-Maxima aufweisen. Die in den Abb. 1 und 4 dargestellten Maxima erscheinen mit Ausnahme des Spätherbstes und des Frühwinters zu allen Jahreszeiten. In ähnlicher Weise gibt es auch keine Synchronisation zwischen den vier Arten mit den zwei Maxima im Jahr. Die Cryptostigmata-Gemeinschaft als Ganzes ist deshalb numerisch stabil, die beobachteten Individuenzahlen variieren lediglich zweimal, zwischen 1732 im Januar (925 davon gehörten zur Art *Tectocepheus velatus*) und 3299 im Mai (als 1548 davon zur Art *T. velatus* gehörten).

(II) Es gab eine vertikale Stratifikation der Gemeinschaft. Vier Arten, *A. poppei*, *C. bipilis*, *C. segnis* und *C. spinifer*, und *Eupelops* spp. wurden gewöhnlich nur im L-Subhorizont gefunden und nur gelegentlich wurden Exemplare (dieser Arten) mehr als 1 cm tief im Fermentationshorizont (F-Subhorizont) gefunden. Alle diese Arten tendierten zu relativ geringen Abweichungen in der Tiefe ihres Vorkommens. Fünf weitere Arten kamen im L- und oberen F-Subhorizont vor und deshalb waren die Tiefenabweichungen dieser Arten größer. Diese Arten sind *C. schützi*, *O. lanceolata*, *P. peltifer*, *S. magnus* und *T. velatus*. Weitere drei Arten, *N. nana*, *P. piger* und *P. spinosa*, waren für die Fermentations-Subhorizonte charakteristisch.

(III) Zwei Faktoren scheinen dafür verantwortlich zu sein, daß die Milbe im Bodenprofil in die Tiefe wandern und es erscheint unwahrscheinlich, daß irgendwelche (anderen) Faktoren die Tiefenwanderung der Milben verursachen. Die tieferen Bodenschichten bieten mehr konstante Umweltbedingungen, obwohl sie einen geringeren Porenraum aufweisen. Die beiden Faktoren, die als Ursache der Vertikalmigration ermittelt wurden, waren beide Extreme der Umweltsbedingungen in der oberen Streuschicht. Während des Winters sanken die Temperaturen und die Streuschicht gefror. Verschiedene Milben, besonders *C. schützi*, *N. nana*, *O. lanceolata*, *P. piger*, *P. spinosa*, *S. magnus* und wahrscheinlich *T. velatus* erschienen in dieser Jahreszeit tiefer im Boden. Während des Sommers 1966 gab es ungewöhnlich geringe Niederschläge, mit dem Resultat, daß der Boden sehr trocken wurde, speziell die Streuschicht (L) und die obere Fermentationsschicht (F). Einige der Milben, *C. schützi*, *N. nana*, *Eupelops* spp. und möglicherweise *A. poppei*, erschienen in dieser trockenen Periode in tieferen Bodenschichten. Es wird erkennbar, daß diese beiden Einflüsse, sehr niedrige Temperaturen und Austrocknung der Bodenoberfläche, nur auf wenige Arten einwirken und daß sie nicht allein auf Arten der Streuschicht (L), sondern auch auf Arten wie *N. nana* einwirken, die für den Fermentations-Subhorizont (F) charakteristisch sind.

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